INTROGRESSION OF *SALVIA APIANA* AND *SALVIA MELLIFERA*

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Salvia apiana and *Salvia mellifera* are two common species of sage in coastal California. Over much of their overlapping ranges they give little or no indication that they can (and frequently do) hybridize and that their hybrids are quite fertile. These significant facts were called to scientific attention by Epling. After monographing these and other Salvias taxonomically (Epling, 1938), he studied them experimentally in the field and in the breeding plot. He demonstrated (Epling, 1947) that they hybridize readily when artificially cross-pollinated and that the resulting hybrids are fertile enough to yield variable F-2's and back-crosses. Though these two species grow closely intermingled over thousands of square miles he found little evidence that hybridization did take place except under disturbed conditions. This he interpreted as due to a complex of internal and external barriers. One of the most important is the different adaptive mechanisms for insect pollination in the two species, S. *apiana* being pollinated largely by bumble bees and S. *mellifera* by small solitary bees.

The problem seemed such an interesting one that the senior author has studied it repeatedly and intensively in the field for somewhat over a decade and has used these two species as field and laboratory material for a summer school course. Population samples from critical areas were pickled for laboratory study, and with the help of the junior author an exhaustive analysis of variation in pubescence, calyx shape, corolla shape, and inflorescence branching was undertaken. This confirms and extends Epling's experimental and field studies. It analyzes a little more precisely the conditions under which the barriers break down between the two species. Thanks are due to Carl Epling, to Harlan Lewis, and to E. G. Anderson for assistance in making the collections.

In addition to the various facts collected by Epling, careful study of two quite different matters seemed necessary before we could interpret the hybridization dynamics of these two species: (1) a more complete morphological analysis of the two species and their intermediates; (2) a precise investigation of the disturbed habitats in which intermediates were common.

Morphological Analysis of Species Differences

If one is effectively to analyze the variation pattern in populations where hybridization is known or suspected, the first *desideratum* is a thorough understanding of the nature of the differences between the hybridizing entities. *Salvia apiana* and *Salvia mellifera* are well-differentiated species, distinguishable at a glance, but if we are to use this difference as a yardstick in measuring what is happening in populations, we must refine our understanding of it to the point where we can distinguish S. *mellifera* with eight ancestors out of eight belonging to

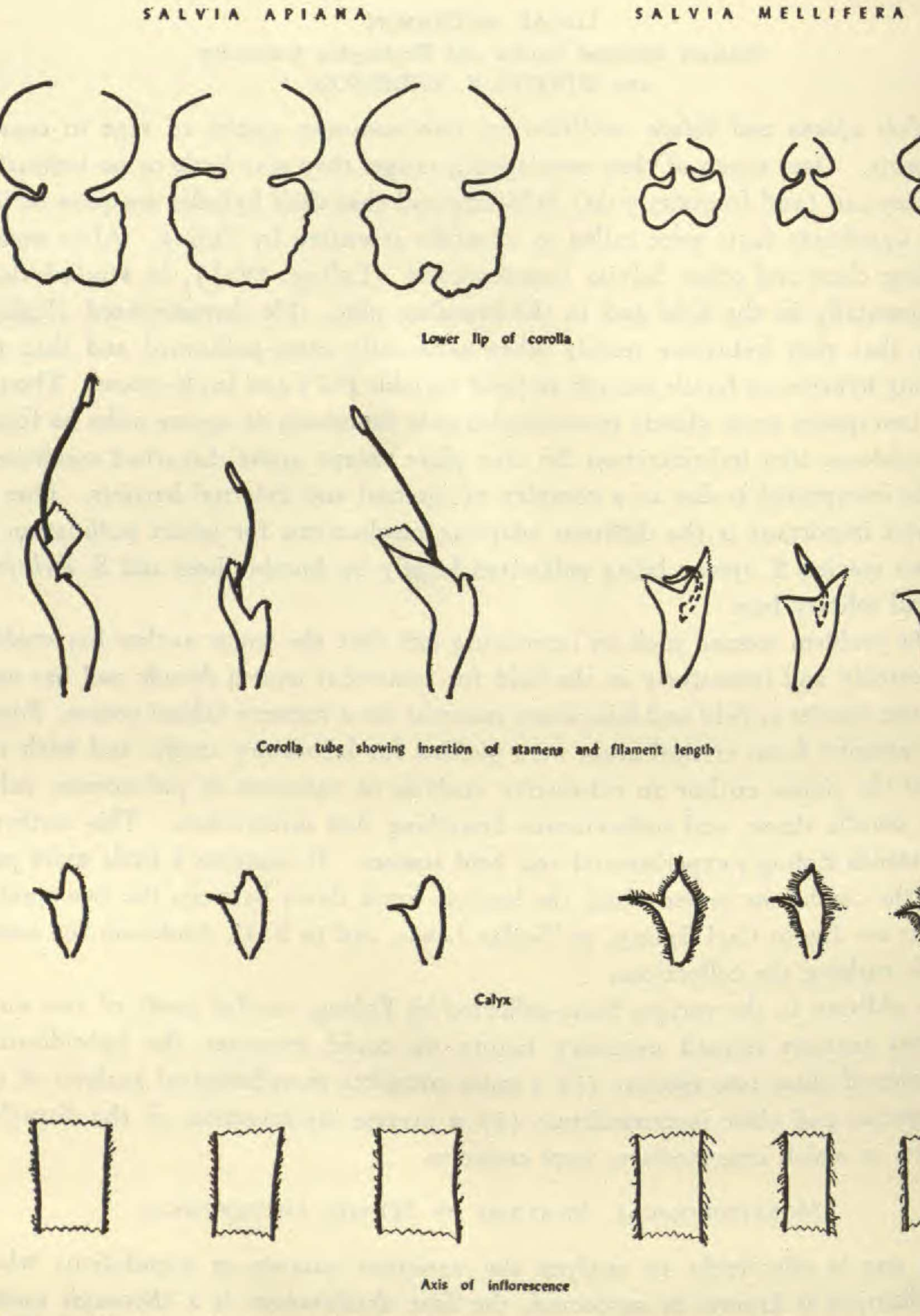

Fig. 1. Drawings of portions of *Salvia* flowers used in analyzing variation pattern. Comparable portions of three plants of *Salvia apiana* and three of *Salvia mellifera* were drawn to scale with camera lucida. Upper row (× 2); second row (× 2) showing filament lengths and position of stamen insertion in corolla tube; third row, calyx × 2), showing length of terminal spine and length of pubescence; bottom row (× 8), view from the side showing length and direction of pubescence.

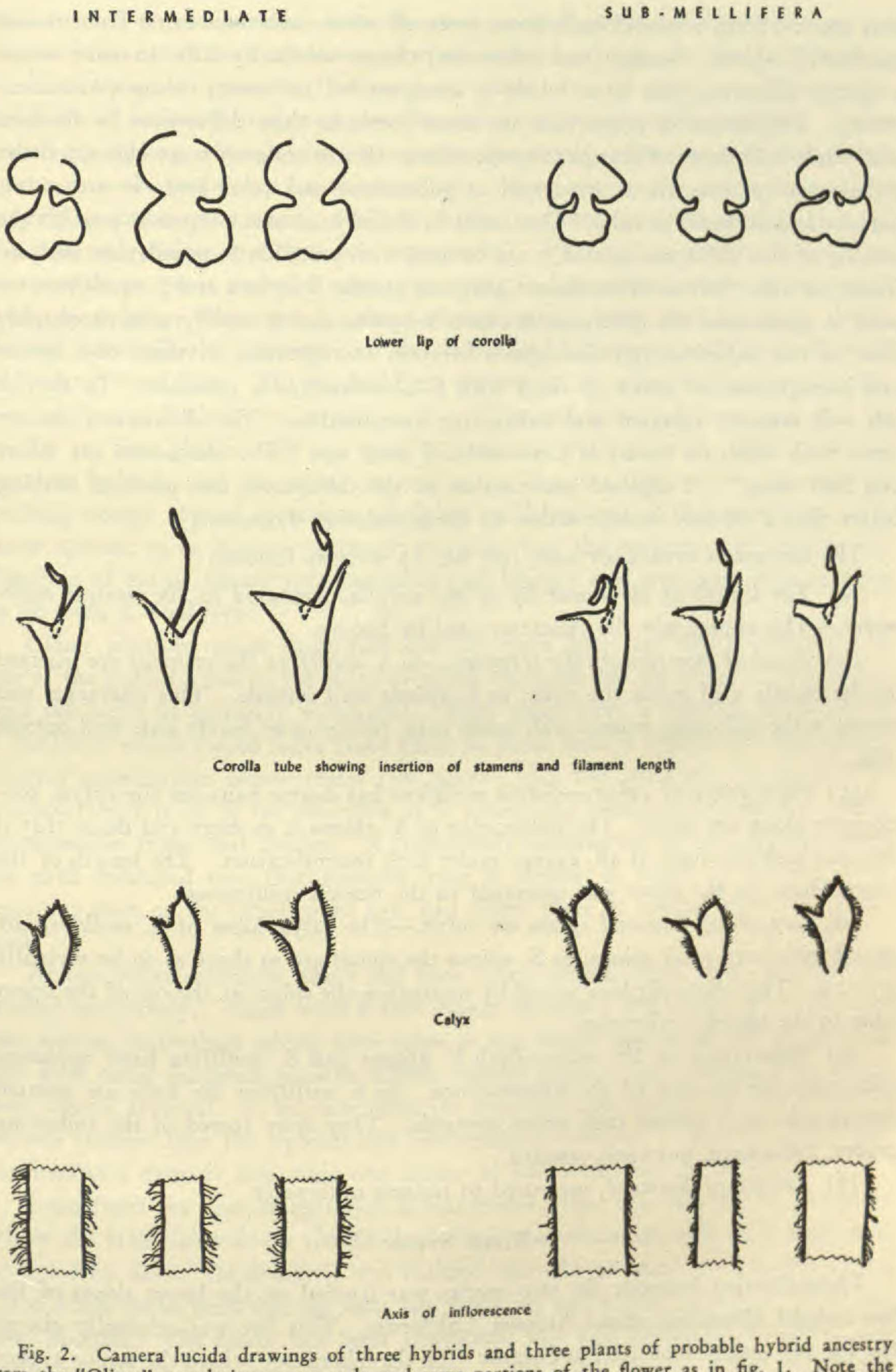

Fig. 2. Camera lucida drawings of three hybrids and three plants of probable hybrid ancestry from the "Olives" population; same scale and same portions of the flower as in fig. 1. Note the intermediacy of the plants at the left compared to those in fig. 1. The plants to the right, when compared with the examples of *S. mellifera*, are typical of the variation pattern produced by introgression. Note that though all three are similar to normal *S. mellifera*, they are more variable, and their slight departures from the average are mostly *in the direction of S. apiana.*

that species, from a second back-cross seven of whose ancestors came from it and one from S. *apiana*. Species (and subspecies) characteristically differ in many ways; a species difference seen as a whole is compounded of many things (Anderson, 1954). Differences in proportion are more common than differences in absolute size, while differences in change of proportion with size are even more characteristic. Pubescence *patterns* are as important as pubescence and color *patterns* are as important as differences in color. One needs to define in as exact terms as possible the totality of this difference so that it can be used with precision in population analysis. There are other Salvias in southern California besides S. *apiana* and S. *mellifera;* we need to understand the difference between S. *apiana* and S. *mellifera* so thoroughly that we can unhesitatingly distinguish between introgression of these two species and introgression of either of them with S. *clevelandii,* for instance. To do this job well requires repeated and exhaustive examination. The differences do not come with labels on them; as Linnaeus said long ago, "The characters are where you find them." A slipshod examination of the differences can produce nothing better than a slipshod interpretation of the population dynamics.

The characters eventually used (see fig. 1) were as follows:

(a) *The length of the lower lip of the corolla, measured to the nearest millimeter.*—This is precisely the character used by Epling.

(b) *Point of insertion of the stamens.*—In S. *mellifera* the stamens are inserted on the corolla well inside the tube; in S. *apiana* well outside. This character was scored in the following grades: well inside tube, barely in or barely out, well outside tube.

(c) *Pubescence of calyx.*—*Salvia mellifera* has coarse hairs on the calyx, particularly along the veins. The pubescence of S. *apiana* is so short and dense that it does not look like hairs at all, except under high magnification. The length of the longest hairs on the calyx was measured to the nearest millimeter.

(d) *Length of terminal spines on calyx.*—The calyx lobes of S. *mellifera* are tipped with long weak spines; in S. *apiana* the spines are so short as to be virtually invisible. This character was scored by measuring the spines at the tip of the upper lobes to the nearest millimeter.

(e) *Pubescence on the axis.*—Both S. *apiana* and S. *mellifera* have appressed pubescence on the axis of the inflorescence. In S. *mellifera* the hairs are pointed downwards; in S. *apiana* they point upwards. They were scored in the following grades: downward, outward, upward.

(f) *Length of filament,* measured to nearest millimeter.

Field Study

Hybridization between the two species was studied on the lower slopes of the San Gabriel Mountains above Arcadia, California. This site was originally chosen not for any special features but because (for the laboratory where the senior author was working) it was the closest spot at which the two Salvias could be found in profusion. They were studied mainly along a footpath which wound westwards (more or less on the contour) from the road up the Santa Anita Canyon. Less intensive field studies were carried on at several other locations. In this area the slope of the mountains is prevailingly toward the south. It is so steep as to approximate the pitch of a church roof, and the thin soil is stony with rock particles. As reported by Epling, though the two species frequently grow intermingled, *Salvia apiana* showed a preference for the drier sites. Along the steepest and jutting ridges, it grew in almost pure stands, while in shadier and moister spots along sections of the trail only *Salvia mellifera* was represented. The trail is one much used for recreational purposes and the vegetation along it has suffered repeated incursions from the public. Beer cans dot the landscape, particularly near the road. Half-formed side-trails are common, and the shrubs and larger perennials bear the scars of repeated vandalism. The site had been subject to disturbances for some decades, yet the flora as a whole was largely native. Out-and-out weeds were rare and the Salvias (at first glance) did not seem to have mongrelized at all. There were no apparent hybrids, and the casual impression was that for these two species one had nothing except typical specimens of *Salvia mellifera* and of *Salvia apiana*. The latter species, to be sure, is extremely variable, but the variations all tend in the direction of *Salvia apiana* var. *compacta* (see below) and seemingly have nothing to do with *S. mellifera*.

Closer plant-by-plant inspection did not quite bear out this conclusion. In one of the gullies, close to the point at which the path left the road, the vegetation bore the scars of intensive vandalism. Here there were a number of plants of *S. mellifera* which varied more from plant to plant than is typical for this species. Careful examination demonstrates (see below) that this variation (in so far as it is measurable) is all *in the direction of S. apiana* and presumably represents slight introgression from that species. A meticulous examination of every plant along the path indicated that introgression from *S. apiana*, so slight as scarcely to be apparent even to the experienced eye, had taken place at several points along the trail.

At one point, however, there had been much introgression, and this area was studied intensively. There were a few plants obviously intermediate between the two species, and others which were more or less like *S. apiana* or like *S. mellifera* but with color patterns, growth habits, corolla shapes, and inflorescences which were clearly atypical. It was not until the area had been repeatedly visited that it became evident that the hybrids and introgressants formed a compact population confined to a distinct area, only one corner of which abutted on the trail.

Even from the first examination it was evident that this area was at the point where the trail came down the farthest from the mountain side, to a spot once occupied by oaks. Gradually it was realized that the variants were confined to a space where some years ago the oaks had been cut and a small grove of olives had been planted. The olives had been abandoned but had continued to grow, and native vegetation had spread in around them. The upper corner of this area, which was crossed by the trail, had been used repeatedly for camping and some of the trees had been cut. It was in this doubly disturbed spot that most of the strangest-looking hybrids were found, but the entire area in among the abandoned olives, in so far as it had any Salvias, had nothing but atypical ones. Some of them were so grossly atypical as to be readily demonstrable as such in the pictorialized diagram (fig. 3) which takes account of only six measured characters. Some were so similar to *Salvia mellifera* that to demonstrate their introgressive origin would require careful scoring of such evanescent characters as flower color pattern and the angles at which the stamens are held.

ANALYSIS OF VARIATION

Collections were made from every plant abutting on the trail and from the area in among the olives. These were treated as two population samples, "path" and "olives." The data are presented as pictorialized scatter diagrams and as frequency distributions for a hybrid index based on these diagrams in figs. 3 and 4. Drawings to scale are shown in figs. 1 and 2 for a few representative plants. It will be seen that the population along the path is mostly composed of plants of the two species which show little or no indication of introgression but that a few of the S. *mellifera* showed slight introgression from S. *apiana,* about as much as we would expect in a second back-cross (i.e. in plants with seven ancestors from S. *mellifera* and one from S. *apiana*). The "Olives" population is clearly mongrel. Off-type plants are in the majority. Seen as a whole they represent the kind of criss-crossing recombinations of intermediate characters so typical of hybrid populations whether natural or artificial. In the area of the abandoned olive orchard such mongrels are clearly in the majority; had it been possible to score such characters as color pattern it would probably have been possible to demonstrate that they make up virtually the entire population.

DISCUSSION

This example of introgression between S. *apiana* and S. *mellifera* is in some ways the most illuminating of the numerous examples of hybridization in natural populations which have been reported in recent years. Let us summarize the main points. Two species easily hybridized in the experimental plot do not ordinarily hybridize in the field, though they grow intermingled over wide areas. However, in a strange habitat (or collection of strange habitats) adjacent to their natural range, hybrids and their mongrel descendants press in to the virtual exclusion of the parental species. There are several important inferences which can be drawn from this example. The abundance of hybrids in the field, once a habitat is provided in which they are at an advantage, demonstrates that there is no barrier (as such) to hybridization between these species. Hybrids are virtually absent, not because they are not being produced but because when they do occur there is no place for them. The association of which these two Salvias are a part has been through the sieve of natural selection. All kinds of species in it have been continuously selected for getting on with each other; they form a multi-dimensional

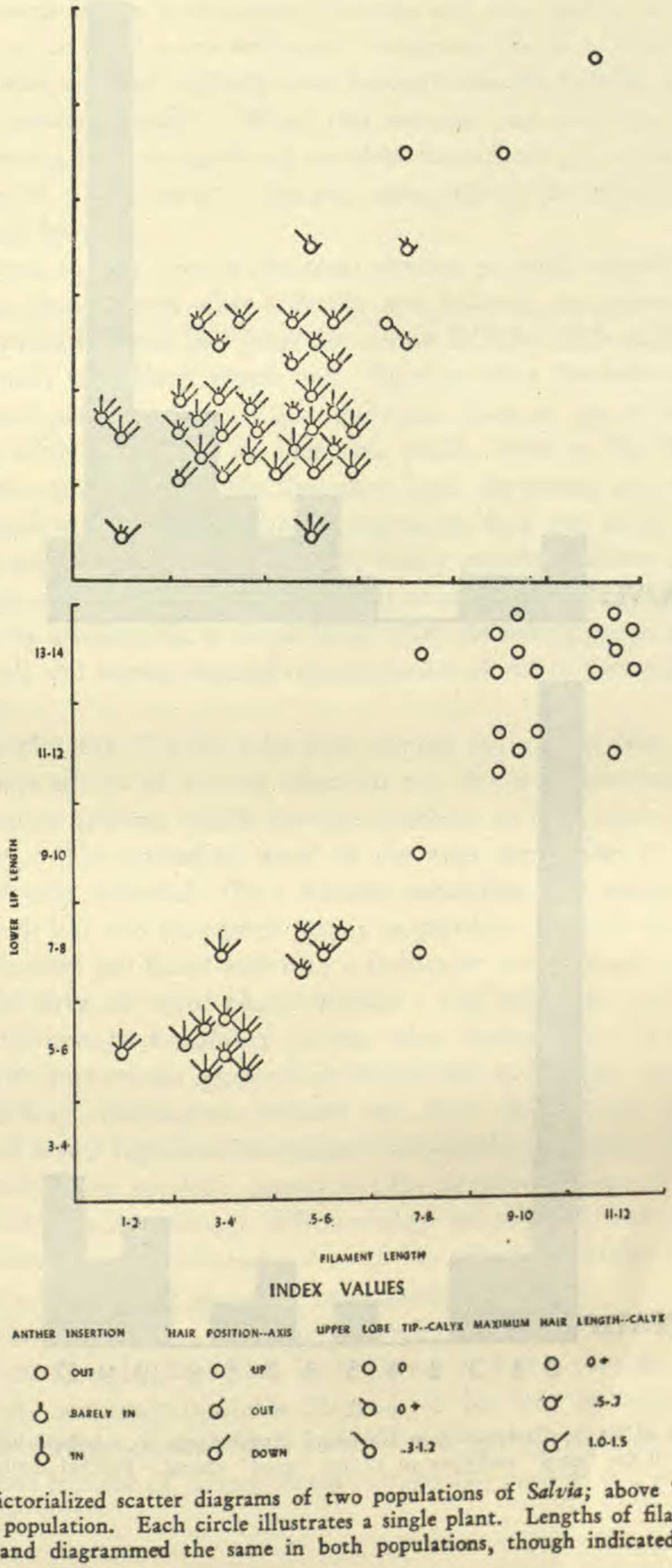

Fig. 3. Pictorialized scatter diagrams of two populations of *Salvia;* above "Olives" population, below "Path" population. Each circle illustrates a single plant. Lengths of filament and of corolla are measured and diagrammed the same in both populations, though indicated only in the lower example.

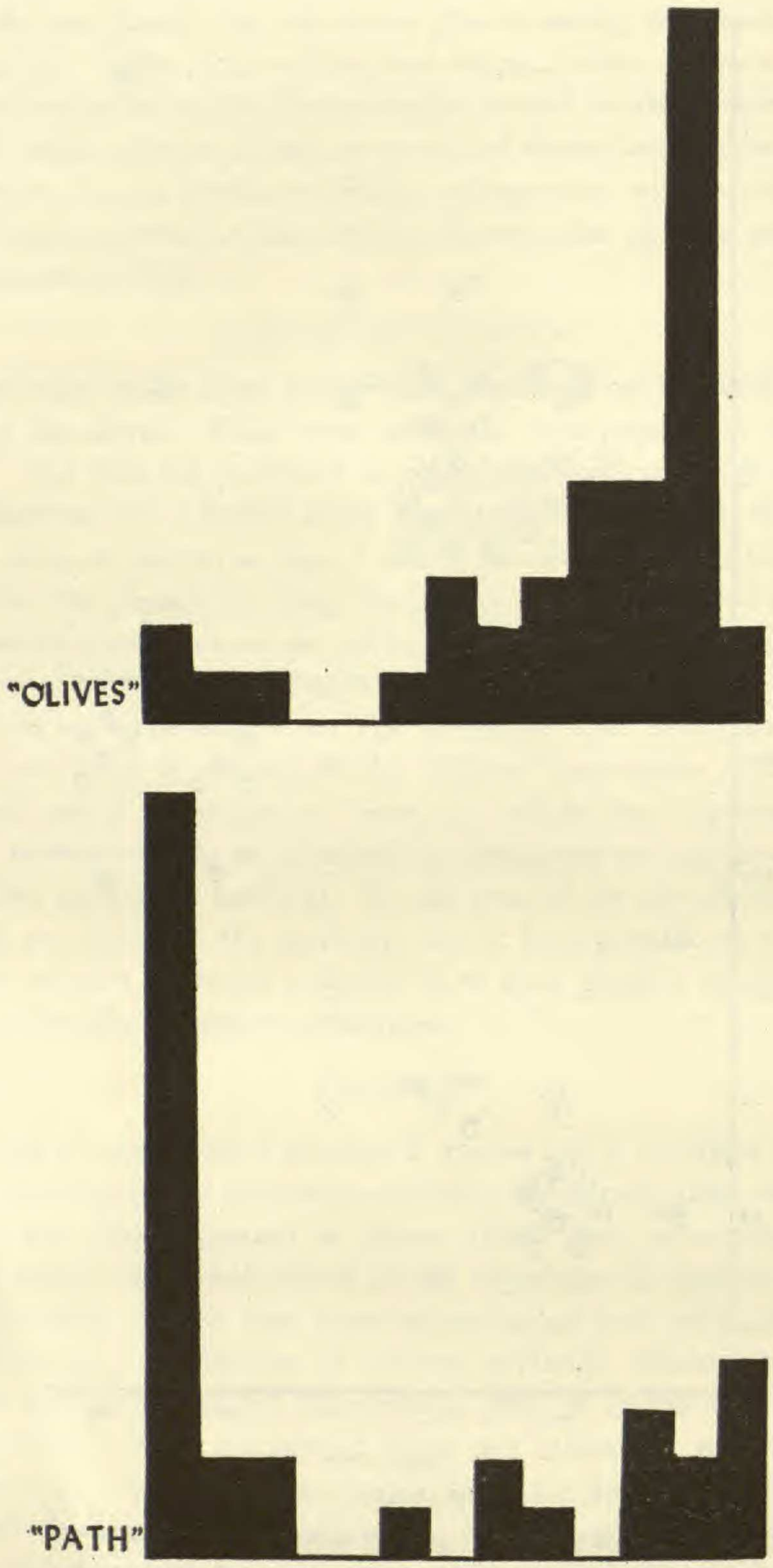

Fig. 4. The data of fig. 3, diagrammed as frequency distributions on a hybrid index which has values running from 0 for "good" *mellifera* to 12 for "good" *apiana*. Further explanation in the text.

jig-saw puzzle the pieces of which fit tightly together. There is no place in this closed association for an intermediate between any two species, or even for minor variants. It is not until a new ecological dominant, like man (Sauer, 1952), comes along and makes a set of radically new habitats that the hybrids can even demonstrate their presence readily. When this happens not only can they grow and persist but among their mongrel and variable descendants are various new recombinations, some of which are at a selective advantage in the relatively open associations produced by man.

By reference to only two of the most obvious physical variables, soil and sunshine, one can demonstrate what radically new habitats are presented by the olive orchard. Previously there had been dry sunny hillsides with pockets of soil, and shady oak woods with black woods soil. Cutting down the oaks and planting the olives produced pockets of sun, shade, and semi-shade on top of black woods soil. Planting out olives introduced an alien tree which, however, had been selected for such Mediterranean climates. On the other hand, the young trees were spaced out away from each other and from woody vegetation in a way quite unlike anything in the native woody flora. It was in these highly peculiar habitats that the variable progeny of the original hybrids had been at a selective advantage. Though we have no proof of the assumption, it seems likely that the hybrid progeny growing there are but a small and highly selected representation of the offspring originally seeded into the area.

It was Darlington (1939) who first pointed out clearly that the short-range and long-range effects of natural selection are almost diametrically opposed and that evolutionary systems which manage somehow to meet both these needs tend to be favored. The immediate need of the next generation is to conserve the adaptation already achieved. In a mature association this means producing offspring as much like the successful parent as possible. In such an association any surviving organism has fitted well into a particular niche; its offspring to succeed as well should have the same characteristics. The long-time need of the species, however, is for enough variability so that when changes arise in the physical and biological environment, the species is at length able to fit into a new niche, or even into new niches. Darlington pointed out how the side-by-side operation of apomictic and sexual reproductive systems in various plant genera allowed the successful individuals to produce, apomictically, offspring which were exact copies of the successful parent, though still retaining the capacity (by sexual reproduction) to produce variable descendants some few of which might be at a selective advantage in a changed or changing environment.

As more and more cases of introgressive hybridization have been analyzed, it has become increasingly clear that such genera as *Salvia* provide an almost ideal solution for this seemingly insoluble dilemma. It has been demonstrated repeatedly (and with increasing clarity) that hybrids and back-crosses are rare in natural populations not because of strong sexual barriers but because in mature associations of plants and animals which have evolved in each other's presence the whole association is closed. It is a complex interlocking system of mutually accommodating niches. Hybrids and back-crosses are absent not because they cannot arise but because when they do there is no place for them. Let man arrive and throw the whole association out of balance; let mammalian herbivores (as in New Zealand) be unleashed upon a vegetation with no previous experience of such beasts, and mongrel populations press into the new niches which have been created and themselves take part in building up a new interlocking system. Those genera, therefore, are at an over-all selective advantage which can build up complex barrier systems of exterior agents (in the wide sense) that protect the successful adaption from change so long as the association of which it is a part goes along its old ways, and yet can spawn hybrids and back-crosses in direct proportion to the breaking up of the old association. Genera with very strong internal barriers (such as complete hybrid sterility between well-differentiated taxa) would eventually perish under such changes and doubtless have.

Summary

1. Introgression between *Salvia apiana* and *Salvia mellifera* (previously studied in the field and in the breeding plot by Epling) was studied intensively in the San Gabriel Mountains.

2. As previously noted by Epling, the two species, though highly interfertile, intergrade only slightly or not at all, even when growing intermingled over very wide areas.

3. Extensive introgression was discovered in a small localized area. It proved to be an abortive olive orchard established some years ago among live oaks adjacent to the mountain side where the Salvias were native. Among these olive trees hybrids and back-crosses between these two species grew in abundance and even formed the bulk of the population.

4. The evolutionary significance of these facts is briefly discussed.

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